The mechanistic basis of population models with various types of competition

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1   Introduction

The population dynamics of single species with seasonal reproduction are often modeled using difference equations $x_{t+1} = f(x_t)$, in which the expected population size x_{t+1} in generation $t + 1$ is expressed as a function of the population size x_t in generation t. In most studies, these models have been introduced as top-down, phenomenological models without sufficient mechanistic basis on individual level. Deriving population models from processes on individual level is an effective way to revel possible mechanisms that underlie these models. Recently, extending Royama's method[1] in deriving the Ricker model from local competition between individuals, first-principles derivations of various discrete-time population models have been presented employing site-based frameworks[2, 3, 4, 5]. Major population models derived in [4, 5] are presented in Tabel 1. These models were derived by assuming that the competition type between individuals was either scramble or contest.

In this article, we present a derivation of a new population model that incorporates these population models as special cases, by considering partitioning of resource between individuals[6]. The model derived has two parameters relating to the type of competition and spatial aggregation of individuals respectively, and it provides a unified view about relationships between various population models in terms of the two parameters.

Table 1: Major population models derived in site-based frameworks.

type	distr.	model	see Eq.	name
scramble	R	$k_1 x_t \exp(-k_2 x_t)$	(15)	Ricker
	N	$k_1 x_t/(1 + k_2 x_t)^d$	(12)	Hassell
contest	R	$k_1[\,1 - \exp(-k_2 x_t)\,]$	(16)	Skellam
	N	$k_1[\,1 - (1 + k_2 x_t)^{-d}\,]$	(13)	Brännström-Sumpter[4]
	N	$k_1 x_t/(1 + k_2 x_t)$	(19)	Beverton-Holt

In the column 'distr.', assumed types of distribution of individuals over the resource sites are specified. R, random (Poisson) distribution; N, negative binomial distribution.

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2 Site-based framework

This study is based on a site-based framework[2, 3, 4, 5], which we will describe in the following. Consider a habitat consisting of n resource sites over which x_t individuals of single species are distributed in generation t. We assume that the expected number of offspring emerging from each site depends only on the number of the individuals at the site. We let $\phi(k)$ be the expected number of offspring emerging from a site containing k individuals. This function is referred to as the interaction function. All individuals emerging from all the sites disperse and are distributed over the resource sites again. These individuals form a population in generation $t + 1$. The expected number of individuals in generation $t + 1$ is written as

$$x_{t+1} = n \sum_{k=1}^{\infty} p_k \, \phi(k), \tag{1}$$

where p_k denotes the probability of finding k individuals at a given site. The distribution p_k is a function of x_t and n. Eq. (1) connects the density dependence on a scale of site (patch), $\phi(k)$, with the whole population dynamics. Choosing p_k and $\phi(k)$ determines the explicit form of the discrete-time population model $x_{t+1} = f(x_t)$ for the whole population. According to scale transition theory[7], population dynamics on the whole population scale are, in general, determined by interactions between spatial variations and nonlinear dynamics on the scale of local populations.

As for the distribution p_k, we assume the following negative binomial distribution with expectation x_t/n:

$$p_k = \frac{\Gamma(k + \lambda)}{\Gamma(\lambda)\Gamma(k + 1)} \left(\frac{x_t}{\lambda n} \right)^k \left(1 + \frac{x_t}{\lambda n} \right)^{-k-\lambda}, \tag{2}$$

which corresponds to a situation in which individuals are forming some clusters. Here, λ is a positive parameter, where $1/\lambda$ represents the degree of spatial aggregation of individuals. In the limit as $\lambda \to \infty$, Eq. (2) becomes a Poisson distribution with expectation x_t/n, which corresponds to a situation in which individuals are distributed completely at random. As for the interaction function,

$$\phi(k) = \begin{cases} 1 & \text{for } k = 1, \\ 0 & \text{for otherwise,} \end{cases} \tag{3}$$

was used in [4] for scramble competition, and

$$\phi(k) = \begin{cases} 1 & \text{for } k \geq 1, \\ 0 & \text{for otherwise,} \end{cases} \tag{4}$$

for contest competition. Eq. (3) describes a situation in which each site can maintain only one individual: if two or more individuals share a site, then they fail to reproduce. On the other hand, Eq. (4) describes a situation in which one successful individual gets all of the resource it requires to reproduce and the others in the same site cannot reproduce. A more general interaction function was used in [5] for each type of competition. From these interaction functions, various population models have been derived[4, 5].

3 A model for intermediate competition

3.1 Derivation from resource partitioning

As a new interaction function which exhibits competition intermediate between scramble and contest, and incorporates the interaction functions described in the preceding section as special cases, we propose the following function:

$$\phi(k) = b\frac{\hat{c}^k - c^k}{\hat{c} - c},\tag{5}$$

where $0 < c < \hat{c} < 1$. We refer to the competition type corresponding to this function as 'intermediate competition'. In the following, we present a derivation of Eq. (5) from the viewpoint of resource partitioning. We suppose that each individual has a minimum sufficient resource requirement s to survive and reproduce; if an individual cannot obtain the amount s of resource, it fails to reproduce. We consider resource partitioning in a site which contains k individuals and an amount R of resource. As an intermediate between ideal scramble and ideal contest cases, combining two kinds of resource partitioning, we assume the following way of partitioning: first, an amount $\hat{s}$ is equally given to all the individuals in the site, and then the remaining resource in the site is partitioned in order of their competitive abilities (see Figure 1). If $R - \hat{s}k < (s - \hat{s})m$, the m-th individual in the site cannot obtain the amount s of resource necessary for reproduction, and fails to reproduce. Letting $\phi_m(k)$ be the expected number of offspring reproduced by the m-th individual in a given site with k individuals, we can write $\phi_m(k)$ as

$$\phi_m(k) = b' \int_{\hat{s}k+(s-\hat{s})m}^{\infty} q(R)dR,\tag{6}$$

where b' is a positive constant, and $q(R)$ denotes the probability density that a given site has an amount R of resource. Here, we assume that $q(R)$ is given by an exponential distribution

$$q(R) = \frac{1}{\bar{R}}e^{-R/\bar{R}},\tag{7}$$

where $\bar{R}$ denotes the expected value of R. The interaction function $\phi(k)$ can be obtained by adding up the contributions from all the individuals in the site as

$$\phi(k) = \sum_{m=1}^{k} \phi_m(k).\tag{8}$$

Combining Eqs. (6), (7) and (8), and performing the summation above give the interaction function (5) under the following relations: $b = b'c$, $c = e^{-s/\bar{R}}$ and $\hat{c} = e^{-\hat{s}/\bar{R}}$. The derivation above shows that it is possible to interpret Eq. (5) as a consequence of the exponential distribution (7) and the way of resource partitioning which is intermediate between exactly equal partitioning and that in order of competitive ability.

We next derive a population model corresponding to the interaction function (5) for the intermediate competition. Substituting Eqs. (5) and (2) into Eq. (1), and performing the summation give the following population model:

$$\hat{x}_{t+1} = \frac{nb}{(1-\beta)}\left\{\left(1 + \beta\frac{\hat{x}_t}{\lambda n}\right)^{-\lambda} - \left(1 + \frac{\hat{x}_t}{\lambda n}\right)^{-\lambda}\right\},\tag{9}$$
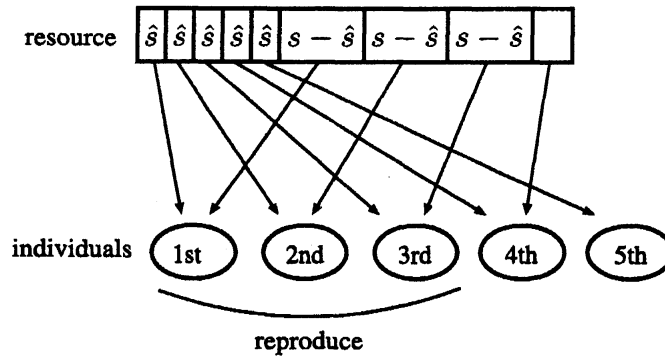
Figure 1: Illustration of the way of resource partitioning in a site for the intermediate competition. At first, each individual equally takes an amount $\hat{s}$ of resource, and then tries to take an amount $s - \hat{s}$ of resource from the remaining resource in order of competitive ability. Only the individuals that are able to get the amount s of resource in total reproduce.

where

$$\hat{x}_t = (1 - c)x_t, \tag{10}$$

$$\beta = \frac{1 - \hat{c}}{1 - c} = \frac{1 - e^{-\hat{s}/\hat{R}}}{1 - e^{-s/\hat{R}}}. \tag{11}$$

Eqs. (9) and (10) show that reproduction curves $x_{t+1} = f(x_t)$ for various values of c are all similar if the other parameters are fixed. As for the parameter β, models with $\beta = 0$ correspond to the case of ideal contest competition, and models with $\beta = 1$ to that of ideal scramble competition. Thus, β can be regarded as the degree of deviation from ideal contest competition.

3.2   Relationships between various population models

The population model derived above, Eq. (9), allows us to understand in a unified way relationships between various population models derived so far in site-based frameworks[4, 5] in terms of two parameters λ and β. Figure 2 illustrates these relationships in a coordinate system of $1/\lambda$ and β. Here, $1/\lambda$ represents the degree of aggregation of individuals, and β the degree of deviation from ideal contest competition. As we describe in the following, various population models can be regarded as certain limit cases of Eq. (9). The limit as $\beta \to 1$ ($\hat{c} \to c$) corresponds to ideal scramble competition, and in this limit, Eq. (9) becomes

$$\hat{x}_{t+1} = b\hat{x}_t\left(1 + \frac{\hat{x}_t}{\lambda n}\right)^{-\lambda-1}, \tag{12}$$

which is the Hassell model. On the other hand, the limit as $\beta \to 0$ ($\hat{c} \to 1$) corresponds to ideal contest competition, and in this limit, Eq. (9) becomes

$$\hat{x}_{t+1} = nb\left\{1 - \left(1 + \frac{\hat{x}_t}{\lambda n}\right)^{-\lambda}\right\}, \tag{13}$$
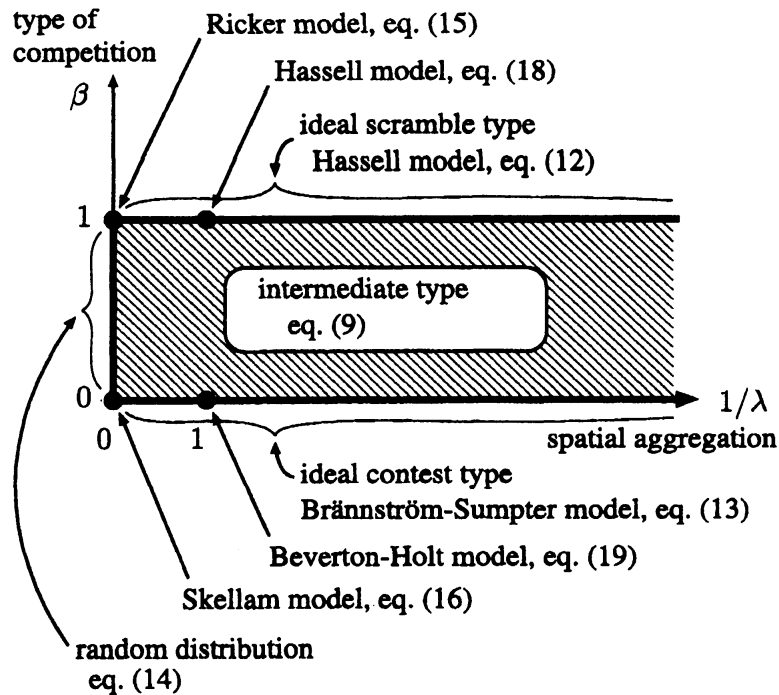
Figure 2: Relationships between various population models are described in a $(1/\lambda, \beta)$ coordinate system. Here, $1/\lambda$ indicates the degree of spatial aggregation of individuals, and β the degree of deviation from ideal contest competition. Various models can be regarded as limit cases of the model of intermediate competition type.

which is the Brännström-Sumpter model[4].

We next consider the limit as $\lambda \rightarrow \infty$. This limit corresponds to the case in which individuals are distributed completely at random over resource sites according to a Poisson distribution. In this limit, Eq. (9) becomes

$$\hat{x}_{t+1} = \frac{nb}{1-\beta}(e^{-\beta \hat{x}_t/n} - e^{-\hat{x}_t/n}). \tag{14}$$

Furthermore, taking the limit as $\beta \rightarrow 1$ ($\hat{c} \rightarrow c$) in Eq. (14) yields

$$\hat{x}_{t+1} = b\hat{x}_t e^{-\hat{x}_t/n}, \tag{15}$$

which is the Ricker model. On the other hand, taking the limit as $\beta \rightarrow 0$ ($\hat{c} \rightarrow 1$) in Eq. (14) yields

$$\hat{x}_{t+1} = nb(1 - e^{-\hat{x}_t/n}), \tag{16}$$

which is the Skellam model.

We next consider the case of $\lambda = 1$, in which the distribution (2) becomes the geometrical distribution $p_k = (x_t/k)^k(1 + x_t/n)^{-(1+k)}$. In this case, Eq. (9) takes the form of

$$\hat{x}_{t+1} = \frac{b\hat{x}_t}{(1 + \beta \hat{x}_t/n)(1 + \hat{x}_t/n)}. \tag{17}$$

Taking the limit as $\beta \to 1$ ($\hat{c} \to c$) further in Eq. (17) gives

$$\hat{x}_{t+1} = \frac{b\hat{x}_t}{(1 + \hat{x}_t/n)^2},$$ (18)

which is the Hassell model. On the other hand, taking the limit as $\beta \to 0$ ($\hat{c} \to 1$) in Eq. (17) gives

$$\hat{x}_{t+1} = \frac{b\hat{x}_t}{1 + \hat{x}_t/n},$$ (19)

which is the Beverton-Holt model. As we have shown above, various population models can be obtained from the model (9) in various limits with respect to the two parameters λ and β.

4 Conclusions

By considering partitioning of resource between individuals in each site, and distribution of individuals over the sites, we have derived a new discrete-time population model for a competition type intermediate between scramble and contest. The derived model incorporates various population models as limit cases in terms of two parameters relating to the type of competition and the degree of spatial aggregation of individuals respectively. In this sense, the model provides a unified view about relationships between these population models in terms of the two parameters.

References

[1] T. Royama. *Analytical population dynamics*. Chapman & Hall, London, 1992.

[2] D. J. T. Sumpter and D. S. Broomhead. Relating individual behaviour to population dynamics. *Proc. R. Soc. B*, 268:925–932, 2001.

[3] A. Johansson and D. J. T. Sumpter. From local interactions to population dynamics in site-based models of ecology. *Theor. Popul. Biol.*, 64:497–517, 2003.

[4] Å. Brännström and D. J. T. Sumpter. The role of competition and clustering in population dynamics. *Proc. R. Soc. London B*, 272:2065–2072, 2005.

[5] M Anazawa. Bottom-up derivation of discrete-time population models with the Allee effect. *Theor. Popul. Biol.*, 75:56–67, 2009.

[6] M Anazawa. The mechanistic basis of discrete-time population models: the role of resource partitioning and spatial aggregation. *Theor. Popul. Biol.*, in press.

[7] P. Chesson. Making sense of spatial models in ecology. In J. Bascompte and R. V. Sole, editors, *Modeling Spatiotemporal Dynamics in Ecology*, pages 151–166. Springer, 1998.